The effect of the host on the morphology of certain species of Gymnosporangium

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(WITH PLATES 28 AND 29)

The large number of rather closely related species of *Gymnosporangium* which have been described as infecting such host plants as the red cedar, *Chamaecyparis*, the juniper, etc., on the one hand, and the hawthorns, apples, shad-bush, etc., on the other, raises the question as to the relation of the particular host to the specific differences in the parasite.

It is commonly accepted (17, 18) that certain species of *Gymnosporangium* gain entrance into the tissues of the coniferous host through leaf infection. In the case of *G. macropus* on the red cedar, strictly foliicolous galls are often quite numerous. To what extent species of *Gymnosporangium* are perennial and whether in such cases sori may develop on the leaves as well as on the branches or trunk does not appear to have been definitely determined in many species. Reed and Crabill (18) claim that the mycelium of *G. macropus* never penetrates beyond the base of the leaf into the twig. The leaf forms which Farlow (3) referred to *G. clavipes* were later found to belong to *G. nidus-avis*, now believed to develop on all parts of the red cedar. When the trunk or branches are attacked the bark is split open or deeply furrowed. The same species may produce the witch's-broom or bird's-nest malformations, and isolated sori may even be found at the base of the leaves or possibly on the leaves themselves. Farlow and Thaxter, in their later publications (4, 20–22), cleared up the points relating to the identity of *G. nidus-avis*, so that one is not left in doubt as to their conceptions of the variations and limitations of this "multiform species."

I am studying a somewhat similar case in connection with *G. biseptatum*, which is perennial in the branches or trunk of *Chamaecyparis*. The teleutospores are commonly three- or four-celled,

but there also occur numerous two-celled spores mixed in with the others. Certain specimens confined to the leaves were distributed by Seymour and Earle as *G. biseptatum* var. *foliicolum* (Econ. Fungi *244*). Ellis also found this variety at Newfield, New Jersey (N. Am. F. *1479*). Farlow's comments clearly set forth the essential facts in regard to the two forms, and I quote the following paragraph from his early work on the *Gymnosporangia* of the United States (3): "The spores of the present species (*G. biseptatum*) are characterized by the great variability in the number of cells of which they are composed. The most usual number is three or four, two are rather common and occasionally there are as many as six. . . . The spores of the present species when full grown are not easily mistaken for those of any other species, but the young tufts on the leaves often bear spores which are all, or nearly all, two-celled. I have received specimens from Mr. Ellis, with the fungus confined to the leaves, and it was difficult to say to what species to refer it. Large sets of specimens collected at Newton, however, show that while the young spots on the leaves may have principally two-celled spores, those on the smaller branches have about an equal proportion of two- and three-celled spores, and the still older branches have a large proportion of three-celled spores. In short, the variability is so great that without a large set of specimens, one would have difficulty in convincing himself that the extreme forms belonged to the same species." It should be noted that Farlow has apparently seen spores with more than two cells in the leaf sori. Thaxter (20) first showed the connection between *G. biseptatum* and *Roestelia Botryapites* on *Amelanchier*, but I do not find that he produced the infection by using spores from sori on the leaves.

Kern (9) describes this leaf form on *Chamaecyparis* as a new species under the name *G. fraternum*, on the basis of "its habit and morphological characters distinct from *G. biseptatum*."

Jackson (8) and Meineke (12) have found witch's-brooms on *Libocedrus*, supposed to be caused by *G. Blasdaleanum*, which has hitherto been thought to be strictly foliicolous (9, 10). Jackson used spores from such specimens and found that the aecidia produced were the same as those derived from infections with spores from the leaf form. This species furnishes an example of

a most striking case of uniformity in the characters of the aecidial stage when developed on hosts of different genera. O'Gara (13) and Jackson (8) have been able to infect species in six different genera of the apple family with this rust. *Malus*, *Pyrus*, *Sorbus*, *Cydonia*, *Amelanchier* and *Crataegus* are susceptible. The constant uniformity of the aecidia on these different hosts, and their "conformity to type" of well authenticated specimens of this rust are their main reliance in assuming that they are working with *Gymnosporangium Blasdaleanum* on the *Libocedrus*.

On the other hand, Pammel (14) has given some data relative to the variations occurring in the aecidiospores and peridial cells when the aecidia of *G. macropus* are found on different host plants. The conditions under which his experiments were made are not given. He reports the infection of the wild crab and *Crataegus mollis* with *G. macropus*, and figures peridial cells and spores from aecidia on each of these hosts and on the common apple. There are noticeable differences in the size, form, and markings of these cells. He says: "In *Crataegus punctata* as well as *C. mollis* the peridial cells extend much longer beyond the surface of the leaf, and they are more finely lacerate. In *Pyrus Iowensis* the cups are shorter, darker brown, and the peridial cells do not cling together as in the *Crataegi*. In the cultivated apple the cups are smaller than [on] either of the other host plants. They project but slightly beyond the surface." It is a common practice, where the aecidial host is known to harbor several species of *Gymnosporangium*, to consider the peridial cells as the most satisfactory means of determining the species of rust, just as the markings on the ascospores of certain species of Discomycetes are thought to be good specific characters. It is well known that the cells at the apex of the peridium differ in length from those at the base, but the shape and markings have been assumed to be fairly constant.

Long (11) has also recently reported variations in *Puccinia Ellisiana* when grown on *Viola* and on *Pentstemon*. On the former host the aecidia are from one to four times as long, are greater in diameter, are deeper in color, have more peridial segments, and dehisce more tardily, while the aecidiospores are smaller than when the rust is grown on *Pentstemon*.

On April 29, 1911, I accompanied Dr. F. D. Kern (see Arthur, 1a) to Newfield, New Jersey, where we found a few specimens of *Gymnosporangium fraternum* in Holton's swamp, and also a quantity of *G. biseptatum*.* Visits made to Newfield and Lakehurst at various times since have afforded opportunity for further study of this stage of the rust.

During the first week in January the most careful inspection of several small marked cedars in the field failed to disclose any positive evidence of infection. Some of the leaves were slightly discolored or bore yellowish spots which contained what appeared to be a resinous substance but no spores. By the middle of March there were many leaves which were of a light waxy-yellow color throughout, and occasionally one could find, with the aid of a lens, lines of eruption from which teleutospores were just emerging. Sori were fully developed by the second week in April. The discoloration of the entire leaf seems to be confined to those which later bear very large sori. Where the sorus is comparatively small (PLATE 28, FIG. 1) the unoccupied parts of the leaf remain green. Infected leaves die off after the sori have disappeared through gelatinization. On June 1, 1914, it was not difficult to find sori, but they showed that in spite of the fact that it had been a very dry season, they had been previously swollen. Spores from these sori gave a low percentage of germination.

Greenhouse cultures, described later, indicate that the development of the sori can be hastened by at least two months. On the other hand, if small cedars are brought in from nature in the last week of March the "forcing process" is not especially effective. The same is true for *G. biseptatum*. Living branches with the fusiform swellings were obtained from Newfield March 21 and kept well watered and sprinkled. The first spores available for inoculation were ready April 13. At this time in nature their condition was much more satisfactory.

There is a great amount of variation in the shape, size, and the thickness of the walls of the spores of the foliicolous form. I have

* I shall use the name *G. biseptatum* to designate the perennial form now sometimes called *G. Botryapites*, and distinguish the foliicolous form on the same host by the name *G. fraternum*, since it will appear from what follows later that there must still be some uncertainty regarding the connections of the original "type," *Roestelia Botryapites*.

not found spores that had more than two cells. Kern (9) states that each cell has two pores near the septum. In the great majority of the spores the upper cell has a pore at the apex, and it is more frequently through this pore (PLATE 29, FIGS. 33–35, 37) that the germ tube appears. The pedicel possesses a characteristic feature noted by Farlow (3) in his discussion of "*G. clavipes*." The "collar," which remains attached to the lower end of the spore after the pedicel has swollen and has more or less disappeared through gelatinization, is apparently the upper portion of the stalk cell wall which becomes disorganized for the most part when moistened. The upper end still persists along with the protoplast which is seen as a long thread-like appendage. The stalk cell is originally cylindrical as described by Kern (9), but when moistened it frequently becomes carotiform (FIG. 26), resembling in this condition the pedicel of *G. clavipes*, though the thickening is much less noticeable. The two-celled spores of *G. biseptatum* resemble in every respect the spores of *G. fraternum* (FIGS. 31, 32).

On April 19, 1914, I found at Newfield a large quantity of *G. fraternum* on seedlings of *Chamaecyparis* a few inches high as well as on trees of all sizes. In a few cases the same branches bore both *G. biseptatum* and *G. fraternum*. The latter also occurred on small trees which were at the same time heavily infected with the witch's-brooms of *G. Ellisii*. At the place where *G. fraternum* was the most abundant there was a good growth of *Amelanchier* and *Aronia*. The leaf buds of the shrubs had not opened to any great extent, and there were no indications that the sori of the *Gymnosporangia* had reached sufficient maturity to have swollen and scattered sporidia during any rains that may have occurred previous to this date. The season was somewhat "late."

Infected seedling cedars were brought in and potted, and root sprouts of *Amelanchier*, *Aronia*, and *Pyrus* were also obtained from this locality and from the grounds of the New York Botanical Garden. It required five or ten days for the leaf buds to open sufficiently for these plants to be used for inoculation purposes; at the end of this time the sori on the cedars had also reached maturity.

Inoculations were made in the greenhouse, and the usual

methods, with slight modifications, were employed. Branches of cedar whose leaves bore sori were sprayed and hung over the trial host, which was then covered with a bell-jar for forty-eight hours. Two or three times during this interval the bell-jar was aired out and the plant sprayed. The sori of *G. fraternum* are so small that there is little danger of killing the alternate host by over infection. A larger number of plants can be more easily inoculated with a small supply of teleutospore material if the sori of germinating spores are shaken in a bottle with water so that the sporidia can be sprayed on the plants directly. The infection chamber mentioned by Fromme (5) has been employed with great advantage. This chamber is constructed by uniting five three-foot window sashes in the form of a box; the front sash is provided with hinges. It is large enough to hold fifteen or twenty plants in four- or six-inch pots, and plants up to two feet high can be inoculated easily under such conditions. The chamber can be aired out and the plants sprayed with little trouble. Another advantage to be gained by the use of this apparatus is the opportunity one has of providing similar conditions for several plants of different species which are being tried out. The old method of using leafy twigs instead of potted plants was also employed with more or less success.

The records contained in Table I* include only those cases in which the recently transplanted host lived fifteen days after inoculations were made. The Aronias from Newfield were badly spotted with small insect galls. The percentage of positive results was no doubt reduced on this account. The dates given in the last four columns refer to the time at which this particular stage was first observed although the fungus may have reached this stage some time previously and been overlooked. Where a date is replaced by a question mark (?) the aecidia were not seen until dehiscence was complete.

The plants used in these trials were chiefly species of *Aronia* and *Amelanchier*. As a large number of leaves on plants of these two genera first inoculated soon showed unmistakable signs of

* A preliminary report of this work has been published recently: Dodge, B. O. Relationship between *Roestelia transformans* and *R. Botryapites*. Torreya **15**: 133, 134. Je 1915.

infection, most of the succeeding experiments were carried out to check up the first results.

It is probable that no importance need be attached to the results obtained in numbers 200 and 221. Only one leaf on each apple seedling was infected, and this might have been due to the presence in the greenhouse of young red cedars bearing *G. macropus* and *G. globosum*. No aecidia developed on these leaves. Farlow (3) and Seymour (19) report *Roestelia transformans* on the cultivated apple. The pear and hawthorn were not infected, but as only one or two plants were tested these results are also inconclusive.

The table shows that about 50 per cent. of the Aronias were infected. Three different species were employed and all gave positive results. Aecidia matured on certain plants of *A. arbutifolia* and *A. nigra*, but the fungus on *A. atropurpurea* did not develop further than the formation of the large primary hypertrophies.

The interval between inoculation and the first appearance of the discoloration indicating infection varies from ten to fifteen days. The areas on the *Aronia* are not especially characteristic. They become raised or convexed and are frequently four or five millimeters in diameter (FIG. 3). After some days, ten to twenty, the parts attacked become sunken as the hypertrophies develop into bright green swellings directly beneath the pits. The galls sometimes seem to be three or four millimeters thick, but this apparent thickness is due in part to the pit in the upper surface of the leaf.

The horn-like processes of the galls (FIG. 4) begin to grow out a week or two later, after which the aecidia quickly develop and reach maturity within two months after inoculation. Frequently the development does not proceed further than the formation of the basal galls. The leaf remains in this condition for several weeks and new spermogonia are formed continually on the galls. Normally aecidia are matured whenever the cornute galls are developed.

FIGS. 7 and 8 show a case in which the growing point of a twig has been entirely transformed by the fungus. Eight weeks elasped between the taking of the photographs.

Occasionally infected leaves curl up soon after spermogonia

TABLE I

RECORD OF INFECTION EXPERIMENTS WITH THE FOLIICOLOUS FORM ON *Chamaecyparis* (*Gymnosporangium fraternum* KERN) IN 1914

No.	Trial host	Date inoc.	Spermogonia observed	Hypertrophy	Gall-horns	Aecidia appeared	Aecidia mature
200	*Malus Malus*	Apr. 25	June 15†				
201*a*	*Aronia nigra**	Apr. 23	May 5	May 19	July 28‡		
201*b*	*Aronia arbutifolia* ...	Apr. 23	May 5	May 19	June 5	June 18	June 21
202*a*	*Aronia nigra*	Apr. 25	May 6	June 10	July 1	July 12	July 24
202*b*	*Aronia arbutifolia* ...	Apr. 25	May 6	June 14	July 10	July 15	July 20
203*a*	*Amelanchier intermedia*	Apr. 25	May 6	May 25	June 14†		
203*b*	*Aronia arbutifolia* ...	Apr. 25	May 6	May 19	May 27	June 3	June 10
204	*Pyrus communis* ...	Apr. 25					
205	*Pyrus communis*	Apr. 25					
221	*Malus Malus*	Apr. 27	June 23§				
222	*Crataegus oxycantha* ..	Apr. 27					
242	*Aronia nigra*	May 6					
243	*Amelanchier Amelanchier*	May 6	May 19	May 28§			
245	*Amelanchier intermedia*	May 6	May 20§				
246	*Amelanchier intermedia*	May 6	May 17	June 4	Aug. 20	?	Sept. 10
249	*Amelanchier intermedia*	May 6	May 25§				
250	*Aronia arbutifolia* ...	May 6					
251	*Aronia arbutifolia* ...	May 6					
252	*Aronia arbutifolia* ...	May 6	May 16	May 24	June 12	June 25	July 5
253	*Aronia arbutifolia* ...	May 6	May 17	May 24	June 12	June 20	June 22
254	*Aronia arbutifolia* ...	May 6					
255	*Amelanchier intermedia*	May 6					
256	*Aronia arbutifolia* ...	May 6					
257	*Aronia arbutifolia* ...	May 6	May 19	June 15§			
258	*Aronia arbutifolia* ...	May 6					
259	*Aronia arbutifolia* ...	May 6					
265	*Aronia arbutifolia* ...	May 6					
267	*Aronia arbutifolia* ...	May 6	May 19§				
268	*Aronia arbutifolia* ...	May 6	May 16	May 26	June 6	June 17	June 20
269	*Aronia arbutifolia* ...	May 6					
270	*Aronia arbutifolia* ...	May 6	May 20	June 12§			
271	*Aronia atropurpurea* .	May 11	May 26	June 12§			
272	*Aronia atropurpurea* .	May 11					
273	*Aronia atropurpurea* .	May 11					
274	*Aronia nigra*	May 11					
275	*Aronia nigra*	May 11					
277	*Aronia nigra*	May 11					
278	*Amelanchier intermedia*	May 11					
279	*Aronia nigra*	May 11	May 26	June 12†			
281	*Amelanchier intermedia*	May 11					
283	*Aronia nigra*	May 11	May 26	June 3	June 12	June 20	June 22
284	*Aronia nigra*	May 11					
344	*Aronia nigra*	June 3	June 21	July 20	Aug. 1	Aug. ?	Aug. 14

No.	Trial host	Date inoc.	Spermogonia observed	Hypertrophy	Gall-horns	Aecidia appeared	Aecidia mature
365	*Aronia arbutifolia* . . .	June 3	June 21§				
366	*Aronia arbutifolia* . . .	June 3					
368	*Aronia arbutifolia* . . .	June 3	June 23	July 10	July 14	July 18	July 23
372	*Aronia atropurpurea* .	June 3	June 12	June 28§			
373	*Aronia atropurpurea* .	June 3					
375	*Aronia nigra*.	June 3	June 15	July 12	July 18	Aug. ?	Aug. 10

* Numbers 201*a*–205, and 279 were leafy twigs; all of the others were potted plants.

† Leaves died.

‡ Killed by "mealy bugs."

§ No further growth.

appear (FIG. 10), but the majority are not materially altered in shape (FIG. 12). FIG. 9 shows how the fungus may also attack young twigs below the growing point. A large number of aecidia develop on such malformations and on the fruit when it is attacked.

The aecidia are about one half millimeter in diameter and two to five millimeters in height, tapering gradually to a fine point (FIG. 15). Frequently those on *Aronia nigra* (FIG. 18) are taller. The dehiscence of the peridium is shown in FIGS. 15, 16, and 17. The cells at the apex do not split apart, and, as a result of the laceration of the portion of the peridium below the apex (FIG. 16) and the reaction of the mature cells to atmospheric changes, the top breaks away (FIG. 19), leaving the lower part of the cup fringed with a tangle of cells. The inner surface of a peridial cell is coarsely warted and most of them are pointed. Some have a notch at one end (FIG. 41), showing that they may overlap or dovetail. The only species known to possess such peridial cells is *Roestelia transformans*, the species that produces hypertrophies on *Aronia* such as I have described. The peridium is said (**9**, **16**) to dehisce at the apex first and gradually fall away. It is likely that collectors have failed to note the manner in which the tip end disappears. The galls are green until long after the aecidia are mature and not brownish as one finds them in dried specimens.

The twigs of *Amelanchier intermedia* used in number 203*a* were obtained at Newfield April 19 and inoculated April 25 with sporidia taken from swollen sori of *G. fraternum*. Spermogonia appeared on several leaves May 6. A potted root sprout of *A. intermedia* also from Newfield was used for number 249. At the

time of inoculation, May 6, the leaves were well out. A few infected areas appeared May 25 but no "subicular hypertrophies," projections, or aecidia subsequently developed. Similar root sprouts of *Amelanchier Amelanchier* and *A. intermedia* from the New York Botanical Garden were used in numbers 243 to 246, and 255. Spermogonia appeared on several in each case except in number 255, but the only one to mature aecidia was number 246. On June 4 hypertrophies were visible, which possessed characteristics quite different from those formed on the Aronias. At each point of infection on the *Amelanchier* leaves there were from two to six separate galls which grew to be about one or two millimeters high by July 22 as shown in FIG. 20. During the next three weeks the tubercles elongated slightly (FIGS. 21, 22). Aecidia reached maturity September 10. FIG. 43 shows an optical section of a peridial cell from the central part of an aecidium. The entire surface is smooth. The walls are not always of uniform thickness and the lumen does not appear to extend the full length of the cell. It is difficult to obtain such a view of an outer or inner surface of the cells of the peridia on *Aronia*. Those on the *Amelanchier* do not coil up in water to any great extent and, as they are merely "wavy" in outline, views of all sides may be obtained. Cultures made later show that two or three tubercular galls occasionally coalesce (FIG. 21) forming a solid mass of tissue from which the same number of aecidia develop. The basal gall subiculum on *Aronia* is often conspicuous from the first (FIG. 4). The horn-like parts are secondary. This is also in a measure true for the fungus on *Amelanchier*, where there is a very slight primary swelling, and one can not tell at first just how many ovoid outgrowths, and therefore how many aecidia, will be formed at any particular point of infection.

It is unnecessary to describe this rust as it appears on *Amelanchier* further at this point than to say that in the characters of the peridial cells and in the manner of dehiscence it corresponds very well in general with exsiccati specimens of *Roestelia Botryapites* on *Amelanchier* or to the original description of *R. Ellisii*, which has long been considered a synonym of *R. Botryapites*. In spite of the fact that no *Gymnosporangium biseptatum* was kept in the greenhouse the possibilities of contamination or mixture of

spores in the field at the time of collection were so great that, likewise, I should have attached no importance to these results were it not for the suggestions by Farlow (3) and others of a possible relationship between the ordinary perennial caulicolous form on *Chamaecyparis* and the "annual" leaf form on the same tree.

Comparing "*Gymnosporangium fraternum* on *Aronia*" and "*G. fraternum* on *Amelanchier*" we see two noteworthy differences: (1) the effect on the host; (2) the characters of the aecidia themselves. *Roestelia transformans* ("*Gymnosporangium fraternum* on *Aronia*") sometimes entirely transforms the terminal buds so that a large number of aecidia are produced on a massive gall; the same type of swelling may occur on young branches (FIGS. 7–9). The leaf may be more or less bent or deformed (FIG. 10). The aecidia arise in long horn-like projections of the host. In a majority of cases, however, in my cultures, as noted above, the *Aronia* leaves are not deformed and the primary or basal hypertrophy is not always prominent (FIG. 12).

Each aecidium of "*G. fraternum* on *Amelanchier*" arises from a gall which is more wart-like or ovoid. FIG. 20 shows such galls; the spot in the center of each indicates where the peridium will grow out. FIGS. 21–25 show further stages. The peridial cells are strikingly different in the two forms. They are very long in both cases. The cells from *Amelanchier* are irregularly bent or hypha-like and smooth on both surfaces (FIG. 43), while in those from *Aronia* the inner surface is invariably roughened with several series of warts (FIG. 41). The forms of the galls from which the aecidia arise are such as might be due to the reaction of different hosts to the stimulus of the same fungus.

The published infection experiments with *G. biseptatum* are very few. Certainly the possibility remains that *Aronia* can be infected with sporidia from the perennial caulicolous form. Arthur (1a) reports the infection of *Aronia* with *G. effusum*, and Kern (10) suggests that *G. effusum* and *Roestelia transformans* are possibly connected. Tubeuf, Saccardo, Sorauer, Pammel, and others have published more or less as a fact the connection between *G. Ellisii* and *Roestelia transformans*. I have repeated Fromme's (6) experiments with *G. Ellisii* and easily succeeded in infecting

Myrica caroliniana. Spermogonia appeared in seven days. Aecidia were ripe within four weeks. Four plants of *Comptonia* and ten of *Aronia* were inoculated at the same time in the same chamber, with negative results.

With the alternate hosts of *G. Ellisii* and *Roestelia transformans* known, only one phase of the question has been solved.

It is a common practice in establishing a connection between two phases of a heteroecious rust to rest content when the rust has been carried from one plant to the alternate host. The unsatisfactory state of our knowledge of several species of the genus *Gymnosporangium* is due in large part to the reluctance of investigators to undertake a piece of work involving such a length of time, and beset with difficulties such as they would be confronted with in any attempt to carry back the infection from the aecidial to the telial host. Plowright (17) and Arthur (1) appear to be, so far as I have learned, the only persons who report having carried such work through.

If the *Gymnosporangium* is a perennial then the number of years the telial host must be kept under strict control conditions before inoculations are made is no less serious a question than the time required to allow the rust to make its effects evident.

In case *Gymnosporangium fraternum* is confined to the leaves of the cedar and is annual, the converse infections should not be extremely difficult to get. If, on the other hand, the rust maintains itself in the wood tissues producing sori on new leaves each year, or after a number of years on the trunk or branches, the history of the successful experiment will be a long one. I have undertaken to carry on some work along this line, and in recording the results so far obtained I do not make any claim to have settled the questions involved.

INOCULATION OF *Chamaecyparis* WITH "*Roestelia transformans* ON *Aronia*"

Twenty-one cedars varying in height from four to twenty inches were brought from Newfield in April, 1914, and potted in the soil in which they had been growing. Some of them were heavily loaded with sori of *G. fraternum* at the time; others had only a few; eleven had none, so far as could be found.

Aecidia had begun to ripen on the Aronias (see Table I) about the middle of June and continued to shed spores for some time. The method of inoculation employed consisted in putting several cedars and Aronias bearing aecidia in the infection frame together and, in addition, the cedars were sprayed with aecidiospores. After two days in the frame, the plants were taken out and stacked together on the bench. This treatment was repeated two or three times with some of the cedars at intervals of about a week. No attempt was made to infect the cedars with spores from "*Gymnosporangium fraternum* on *Amelanchier*."

Certain of these cedars were "sunk" in the garden during the month of October and then put in the cold frame; others were left in the greenhouse until December or January and then put in the cold frame; those remaining were kept in the greenhouse all winter.

Beginning about the first week in December the cedars were removed from the cold frame one by one until all had been brought in by March. A very careful inspection of the plants as they were taken from the frame showed that no sori had developed. The results may be summarized under the five groups into which the plants may be divided according to their previous treatment or condition.

TABLE II

INOCULATION OF *Chamaecyparis thyoides* WITH *Roestelia transformans* ("*Gymnosporangium fraternum* ON *Aronia*") IN 1914

Plants free from sori in spring of 1914						Plants having sori in spring, 1914			
Inoculated June, July			Control, not inococulated			Inoc. June, July			Control†
No.	Result	Date	No.	Result	Date	No.	Result	Date	
		(1915)						(1915)	
432	+	Mr. 24	345	0		419	+	Jan. 22	
437	+	Mr. 26	346*	0		347	+	Feb. 7	
400	+	Mr. 29	433	0		404	+	Feb. 19	
445	+	Apr. 22	436	0		421	+	Mr. 5	
406	−		424*a*	0		435	+	Mr. 29	
409	−					348	+	Mr. 30	
						410	+	Mr. 30	
						420	−		
						434	−		
						349	−		

* Numbers 346, 404, 406, 420, 437, and 445 were kept in the greenhouse all winter; the others had been in the cold frame for from one to three months.

† All available plants having sori in the spring of 1914 were inoculated on the questionable assumptions that they would be more susceptible and that the mycelium is annual in the cedar.

The table shows that of the eleven cedars not having sori in 1914 five which were not inoculated developed no sori in 1915. Six were inoculated and four of them bore sori in 1915. Ten plants had sori in 1914 and all of these were inoculated, seven of them producing teleutospores in 1915. The first to show infection had been put in the cold frame October 29 and was brought in December 9. Two sori were discovered January 22. Eight more had been formed on this plant by March 12.

This teleutospore material was used in making further inoculations of *Amelanchier* and *Aronia* to check up the results obtained in 1914. Owing to the limited supply of spores on February 22, the sori of germinating spores were rubbed on the individual leaves of *Amelanchier*. Over infection resulted and many of the leaves were killed. The results of the experiments are given in Table III.

TABLE III

INFECTION EXPERIMENTS WITH SPORES FROM LEAVES OF POTTED PLANTS OF *Chamaecyparis* THAT HAD BEEN INOCULATED WITH *Roestelia transformans* IN 1914

No.	Trial host	Date inoc.	Spermogonia observed	Hypertrophy	Gall-horns	Aecidia appeared	Aecidia mature
425*a*	*Amelanchier intermedia**	Feb. 22	Mr. 6†				
427*a*	*Amelanchier canadensis**	Feb. 22	Mr. 6‡				
441	*Amelanchier intermedia*	Feb. 22	Mr. 6	Apr. 18	May 25	June 10	June 20
449	*Aronia arbutifolia*	Mr. 7	Mr. 18	Apr. 18§			
431	*Amelanchier canadensis**	Mr. 11	Mr. 22‡				
430	*Amelanchier intermedia*	Mr. 13	Mr. 24	Apr. 22	May 23	June 10	June 27
438	*Amelanchier intermedia*	Mr. 13	Mr. 26	May 5	May 20	July 6	July 25
439	*Amelanchier intermedia*	Mr. 13	Mr. 26	Apr. 20	May 25	June 24	June 30
442	*Amelanchier intermedia*	Mr. 25	Apr. 5	Apr. 20§			
443	*Amelanchier intermedia*	Mr. 25	Apr. 10	June 1	June 20	July 4	Aug. 2
444	*Aronia arbutifolia*	Mr. 25	Apr. 12	May 1§			
447	*Amelanchier Amelanchier*	Apr. 14	Apr. 23§				

* Leafy twigs were used in numbers 425*a*, 427*a*, and 431; all others were potted plants.

† Photographed and preserved as specimens.

‡ Infected leaves all killed.

§ No further growth.

There were ten different plants of *Amelanchier* including three species. Two numbers of *Aronia* were also used. The absence of failures may be attributed to the care taken in making the inoculations, and to the vigorous condition of the plants. These experiments (except number 447) were made before any teleutospore

material of *G. biseptatum* was brought into the greenhouse. It requires three or four weeks after aecidia make their first appearance on *Amelanchier* for them to reach their full length. Some of them appear to be unable to force their way out of the gall readily. The peridial cells loosen up so that spores are scattered long before the full growth of the peridium is attained (FIG. 24).

A large quantity of *G. biseptatum* was obtained at Lakehurst, New Jersey, on April 25, 1915. *G. fraternum* was not as abundant here as at Newfield, although scattering infections could be found on almost any *Chamaecyparis*.

Another set of cultures on *Aronia* and *Amelanchier* was made with *G. fraternum* from this locality. A summary of the results is given in Table IV.

TABLE IV

INFECTION EXPERIMENTS WITH *Gymnosporangium fraternum* FROM LAKEHURST IN 1915

Date of inoculation	Species of trial host	Number of plants	Positive results	Negative results
April 29.....	*Aronia arbutifolia*	11	9	2
April 29.....	*Aronia nigra*	5	5	0
April 30.....	*Aronia arbutifolia*	4	4	0
April 30.....	*Amelanchier intermedia*	1	1	0
April 30.....	*Amelanchier Amelanchier*	1	1	0
May 1.....	*Aronia nigra*	1	1	0
May 2.....	*Aronia arbutifolia*	8	6	2
May 2.....	*Amelanchier Amelanchier*	1	1	0
May 3.....	*Aronia arbutifolia*	6	2	4
May 3.....	*Amelanchier intermedia*	3	0	3
May 3.....	*Amelanchier canadensis*	1	1	0
May 16.....	*Aronia arbutifolia*	5	3	2
May 16.....	*Aronia nigra*	4	0	4
Totals.....	*Aronia*	44	30	14
	Amelanchier	7	4	3

Only a small supply of teleutospores was available May 3 and May 16. This in part accounts for the low percentage of infection on these dates. The *Aronia* leaves were rather old to expect good results. Three-fourths of the Aronias were infected and most of them developed a large number of aecidia. Four out of seven Amelanchiers were also infected. While *Amelanchier Amelanchier* was infected none of the plants of this species matured aecidia.

The question of determining whether the caulicolous form

(*Gymnosporangium biseptatum*) is capable of infecting *Aronia* was next considered. Small plants of *Aronia* and *Amelanchier* were in excellent condition at this time and the supply of teleutospore material from Lakehurst, New Jersey, was unlimited. The infection frame was used so that the different species of trial host could be subjected to the same conditions. Several branches bearing telia were hung about in the frame, and the plants were sprayed with large quantities of sporidia. Whenever Aronias were inoculated (except on April 15) one or more plants of *Amelanchier* were also used as controls. Table V also includes the results of experiments carried out in 1914. The teleutospore material used April 13–16 was obtained from Newfield.

TABLE V

INFECTION EXPERIMENTS WITH THE CAULICOLOUS FORM (*Gymnosporangium biseptatum*) IN 1914 AND 1915

Date	Trial host *Amelanchier*	Number of plants	Results +	Results —	Trial host *Aronia*	Number of plants	Results +	Results —
(1914)								
Je. 11	*A. canadensis*	1	1	0	*A. nigra*	3	0	3
" "	*A. intermedia*	1	0	1	*A. arbutifolia*	5	0	5
" "	*A. Amelanchier*	1	0	1				
(1915)								
Apr. 13	*A. intermedia*	1	0	1	*A. nigra*	3	0	3
" "					*A. arbutifolia*	1	0	1
" 15					*A. nigra*	3	0	3
" "					*A. arbutifolia*	10	0	10
" "					*A. atropurpurea*	1	0	1
" 16	*A. intermedia*	1	1	0	*A. nigra*	10	0	10
" "					*A. arbutifolia*	10	0	10
" 26	*A. intermedia*	3	3	0	*A. nigra*	11	0	11
" "					*A. arbutifolia*	8	0	8
" 29	*A. intermedia*	2	2	0	*A. nigra*	1	0	1
" "					*A. arbutifolia*	2	0	2
" 30	*A. intermedia*	6	6	0	*A. nigra*	1	0	1
" "	*A. Amelanchier*	2	2	0	*A. arbutifolia*	3	0	3
" "					*A. atropurpurea*	1	0	1
May 16	*A. intermedia*	11	11	0	*A. nigra*	7	0	7
" "	*A. canadensis*	2	2	0	*A. arbutifolia*	14	0	14
" "					*A. atropurpurea*	1	0	1
Total .	*Amelanchier*	31	28	3	*Aronia*	95	0	95

Some of the Aronias employed in making these tests were used over again for the second or even the third time. The first

sowings were made just as the first leaves were opening. When the last trials were made, May 16, there were still a few new leaves on each plant, but most of the leaves were too old perhaps to be susceptible to any rust. In order to determine this point *G. fraternum* was sowed on nine of the plants the same day (see Table IV) and three infections were obtained.

The variable length of time required for the development of the spermogonia demands that the plants should be kept under control conditions for at least a month. Arthur (2) reports sowing *G. biseptatum* on *Amelanchier canadensis* which did not develop spermogonia until after a period of twenty-five days. One of my cultures, No. 540, required thirty days. This was a shrub of *A. intermedia* about two feet high, which was transplanted from the garden April 28, after its leaves were full grown. *G. biseptatum* was sown on it April 30. The plant did not do well after it was transplanted; the leaves assumed what gardeners call the "sleepy condition." As no spermogonia were visible May 15, the plant was topped to save it. The remaining leaves soon regained their normal rigidity. On May 30 spermogonia began to appear in considerable numbers. Twenty-seven other infections were obtained on *Amelanchier*. Six showed signs of infection on the seventh day; four required eight days; ten showed in nine days; six in ten days; the one infected in the garden required thirteen days. The average incubation time of *G. fraternum* on *Aronia* and *Amelanchier* appears to be between nine and twelve days. Table VI contains a summary of these periods in some sixty experiments with *G. fraternum*.

TABLE VI

INCUBATION PERIOD OF *Gymnosporangium fraternum* ON *Amelanchier* AND *Aronia*

Incubation period, days	6	9	10	11	12	13	14	15	16	17	18	20	22
Number of plants: *Aronia*	3	12	15	5	4	4		1		1	3	1	1
" " " *Amelanchier*		1	1	4	4	3	1	1	1	1			

Gymnosporangium biseptatum (caulicolous form) will infect *Amelanchier* readily, but if it ever infects *Aronia* it must do so under different conditions from those prevailing in connection with the ninety-five attempts which I have made to bring it about.

My experiments of 1914, confirmed by those of 1915, also show that *G. fraternum* will infect *Amelanchier* about as readily as it will *Aronia*, producing on the *Amelanchier* hypertrophies and aecidia which may have furnished the basis for Peck's *Roestelia Ellisii* and which is without doubt now widely distributed in exsiccati under the name *R. Botryapites*.

Leaving aside the question of the accuracy or thoroughness of my experiments in attempting to infect *Aronia* with *G. biseptatum* the other cultures show that the foliicolous form on *Chamaecyparis* occurring so abundantly at Newfield and Lakehurst, New Jersey, is the *Gymnosporangium* connected with the well known *Roestelia transformans*.

GENERAL DISCUSSION

The color of the gall on *Aronia* produced by *Roestelia transformans* is commonly described as red or brownish. To quote from Peck (**15**): "Subiculum much thickened, produced into tufts of crowded subcylindrical or cornute processes, red or brownish, sometimes transforming an entire leaf."

I have noted above that the galls in my cultures remain perfectly green long after the aecidia are mature, and turn brownish only when old or after much exposure to weathering.

In 1875 Peck (**16**) described *Roestelia Ellisii*, collected by Ellis on leaves of *Amelanchier* at Newfield. Peck's description might well have been drawn from the form which I have obtained on *Amelanchier* by inoculation with *Gymnosporangium fraternum*: "Spots yellow, red or brown; subicular projections clustered or scattered, ovate, greenish, or yellowish; peridia cylindrical, single at the apices of projections, the laciniae remaining united at the apex, the cells linear, subflexuous, smooth. . . . This species is related to *R. transformans* Ellis, from which it differs in its paler, shorter, and differently shaped subicular projections, the smooth cells of the peridia, and the apically united laciniae." I have pointed out that in *R. transformans* on *Aronia* the apical peridial cells remain united, falling off together, and that the color of the galls varies with age. Peck could not have known of *R. Botryapites* or had it in mind when he described *R. Ellisii* for all subsequent writers have considered them identical on the basis of the "smooth flexuous cells," and the form of the galls on the host.

The galls of "*Gymnosporangium fraternum* on *Amelanchier*" are at first small wart-like growths, somewhat flattened or depressed at the center (FIG. 20). Ten or twelve weeks after inoculation the pit disappears and the gall begins to elongate, becoming ovoid (FIG. 21). The apex is marked by several rounded prominences (FIG. 25). There are no such fluted collars visible on the galls on *Aronia*. Thaxter (**20**) and Arthur (**2**) report that it requires from four to five months for the complete development of *Roestelia Botryapites* on *Amelanchier*. My records show that it takes about the same time for *Gymnosporangium fraternum* on *Amelanchier*, while on *Aronia* the aecidia mature six or eight weeks after inoculation.

Of the galls produced on *Amelanchier* when infected with *G. biseptatum* Farlow (**4**) says: "Although the peridia are not yet ripe there can be no doubt that the species is *R. botryapites*, as the tubercular swellings produced can not be mistaken for those of any other species known in this country."

I have shown that *G. fraternum* produces an aecidial form on the *Amelanchier*, which resembles very closely the aecidium known as *Roestelia Botryapites*, proved to be connected with *G. biseptatum*. It would be of no consequence whatever to draw conclusions as to the relationship of these two *Gymnosporangia*, based on even the most critical examination of the existing exsiccati of *R. Botryapites* which have all been collected in the field. There could be no assurance that two collections bearing the same number had the same origin. The spots on two leaves in the same package or even two spots on one leaf may have originated from two different teleutospore forms, one from the caulicolous, the other from the foliicolous form. This question can be attacked to greater advantage when a more extended opportunity has been afforded for a comparison of the various stages in their development, side by side on the same plant, of these two aecidia grown under controlled conditions. There are, however, certain hypotheses that may well be stated here with considerations *pro* and *con*.

It is possible that *G. fraternum* and *G. biseptatum* are two distinct species, as it happens, having on *Amelanchier* aecidia much alike. The following points support such a view: (1) the absence

of spores with more than two cells in the sori of *G. fraternum*, and the overwhelming predominance of three- to six-celled spores in *G. biseptatum;* (2) leaves of certain marked cedar trees at Newfield, to my knowledge, have borne sori of *G. fraternum* in the spring season of three years, the first being in 1911, with no indication of there being in the process of formation the fusiform swellings characteristic of *G. biseptatum* on any of the branches in 1913–1915; (3) it is possible to infect both *Aronia* and *Amelanchier* with *G. fraternum*, while *G. biseptatum* regularly infects *Amelanchier* only, so far as known at present; (4) we may have here a case similar to that described by Long (11). The two rusts, *Puccinia Ellisiana* and *P. Andropogonis* have the common teleutospore host *Andropogon*. The aecidial stage of the former is found on *Viola*, that of the latter on *Pentstemon*. Starting with aecidiospores on the violet and going back through the *Andropogon* he is able to infect *Pentstemon* very easily; but when he begins with *P. Andropogonis* on *Pentstemon* he finds that it is much more difficult to infect the violet. He believes that *P. Ellisiana* is continually passing over from the violet through *Andropogon* to *Pentstemon* by natural infections, in which case *P. Andropogonis* is being created over and over again. Once on the *Pentstemon* the rust is probably unable to get back in nature to the violet and therefore becomes fixed as a new form of the old species, *P. Ellisiana*. In addition to the marked changes in the aecidium which I have previously mentioned, Long also finds that the uredospore characters are modified by changing the regular sequence of hosts. *Gymnosporangium fraternum* being able to infect both *Aronia* and *Amelanchier* would correspond to *Puccinia Ellisiana; G. biseptatum*, so far as known being confined to the aecidial host *Amelanchier*, is the new form. In other words, the changes wrought in the morphological characters of *G. fraternum* during its life on *Amelanchier* would be reflected as physiological changes to such an extent that the fungus on going back to the *Chamaecyparis* becomes perennial in the tissues of the branches where further morphological changes are induced. (5) Cedars inoculated by me with aecidiospores of *Roestelia transformans* in July developed sori of *G. fraternum* the following spring, while controls (not inoculated) did not. Dr. E. W. Olive transplanted a small cedar from Newfield to the

grounds of the Brooklyn Botanic Garden April 19, 1914. This cedar bore a witch's-broom of *G. Ellisii* and many leaves showed sori of *G. fraternum*. Dr. Olive has informed me that although sori of *G. Ellisii* have appeared this spring, no *G. fraternum* has been found. This, so far as it goes, suggests that *G. fraternum* is annual.

Against the first of these arguments we have Farlow's statement that the number of cells in the spores of *G. biseptatum* varies according to the size of the branches upon which sori develop—the smaller the branches the greater the number of two-celled spores.

As for the second point it should be remembered that only two converse infections have been reported in connection with this genus. Arthur (1) reports that it requires only one year to complete the development of *G. clavipes* on the common juniper. Plowright (17) shows that *G. clavariaeforme* needs two years. These authors do not state the length of time previous to these experiments the junipers had been under observation so as to preclude the possibility of natural infections. To cite a case in point: a seedling *Chamaecyparis* about four inches high bearing a dozen sori of *G. Ellisii* was brought in from Newfield in May. A month later it was difficult to locate with certainty the region infected. Heald (7) was unable to infect the red cedar with the common apple rust. It is plainly as yet entirely uncertain how long a time elapses between inoculation and the formation of the spindle-formed distortions by *G. biseptatum*.

The behavior of known biological species of other rusts is such as might account for the difference in the susceptibility of *Aronia* and *Amelanchier* to infection by *G. fraternum* and *G. biseptatum*.

Having determined the facts regarding the infection limits of *G. fraternum* and *G. biseptatum* in connection with *Aronia* and *Amelanchier*, the most difficult part of the work still remains to be accomplished if a relationship between the two species of rust is to be established. We must know, first, whether "*G. fraternum* on *Amelanchier*" (*Roestelia transformans?* on *Amelanchier*) goes back to the cedar as *G. fraternum* or as *G. biseptatum* or as both; second, does *G. biseptatum* on *Amelanchier* (*Roestelia Botryapites* on *Amelanchier*) go back to the cedar and reappear as *G. bisepta-*

tum or as *G. fraternum*, or as both. We must also have further confirmation of the experiments recorded above in connection with converse inoculations of the cedar with *G. fraternum* on *Aronia* (*Roestelia transformans* on *Aronia*). Experiments bearing on these points are under way.

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Explanation of plates 28 and 29

FIGS. 1, 3, 13–19, 22–25 from microphotographs taken with a binocular microscope camera, magnifications given under each explanation.

FIGS. 2, 4–12, 20 and 21 from photographs, natural size. FIGS. 26–43 from drawings made with aid of camera lucida, and magnified about 400 diameters.

PLATE 28. *Gymnosporangium fraternum* on *Aronia*, *Amelanchier*, and *Chamaecyparis*

FIG. 1. Sorus on leaf of *Chamaecyparis thyoides;* photographed April 16. × 5.

FIG. 2. Two sori in swollen condition, spores germinating June 3, nearly two months after leaves were collected and dried. Natural size.

FIG. 3. Small leaf of *Aronia nigra* showing group of spermogonia. × 3.

FIGS. 4–6. A leaf of *Aronia arbutifolia* from No. 203*b* (see Table I) showing various stages in the development of basal hypertrophies, horn-like galls, and aecidia. Fig. 4 photographed May 27; Fig. 5 same leaf June 5 with full grown galls; Fig. 6 side view of the same leaf June 20. Natural size.

FIG. 7. Growing point of twig of *Aronia nigra* one month after inoculation. Photographed May 22. Natural size.

FIG. 8. The same twig July 22. The leaves on the lower part of this twig had fallen off early in June, but the gall remained dark green until killed by insects. Natural size.

FIG. 9. Twig of *Aronia nigra* with large gall which later bore many aecidia. June 15. Natural size.

FIG. 10. Leaf of *Aronia nigra* much transformed; basal hypertrophies not noticeable. Natural size.

FIG. 11. Small leaf of *Aronia arbutifolia* infected at both edges; aecidia matured June 24. Natural size.

FIG. 12. Small leaf of *Aronia nigra* not distorted by the fungus. Natural size.

FIG. 13. Tip end of leaf of *Aronia arbutifolia* bearing several horn-like galls. × 3. Compare with FIG. 22, the same fungus on *Amelanchier intermedia*, which is also magnified three times.

FIGS. 14–19. Stages in the growth and dehiscence of a peridium; FIG. 14 the peridium just appearing, very sharp pointed; FIG. 15 the same four days later showing that dehiscence begins at a point considerably below the apex; FIG. 16 the dehiscence is complete, but the apical portion is still intact; FIG. 17 another aecidium from which the apical portion, shown in FIG. 19 has just fallen off naturally; FIG. 18 a long peridium from *Aronia nigra*. × 7.

FIG. 20. Leaf of *Amelanchier intermedia* showing typical appearance of clusters of wart-like galls, slightly pitted at this stage. Compare with FIGS. 4 to 13 of the same fungus on *Aronia*. Natural size.

FIG. 21. Leaf of *Amelanchier intermedia*, galls further advanced and nearly full grown. Slightly reduced in size.

FIG. 22. Portion of the same leaf two weeks later, showing the characteristic knob at the end of each gall; one peridium well out. × 3. Compare with FIG. 13. × 3.

FIG. 23. One gall from the leaf shown in FIG. 21. The knob at the end of the gall is better shown in FIG. 25. × 7.

FIG. 24. Gall with aecidium from leaf of *Amelanchier intermedia;* the lacerations are plainly visible although the peridium has just begun to appear; spores have already been shed in considerable numbers. × 7.

FIG. 25. Gall from leaf shown in FIG. 21; the striations on the peculiar growth at the apex of the gall are visible. Compare with FIGS. 13 to 18 which show that no such structure is formed when the fungus is on *Aronia*. × 10.

PLATE 29. *Gymnosporangium fraternum*, except FIGS. 31 and 32. Magnified 400 diameters

FIGS. 26–30. Teleutospores of *Gymnosporangium fraternum;* Fig. 26, the pedicel is much swollen and the collar is distinctly visible; FIG. 27 shows that the germ pore may be at the apex of the upper cell; FIG. 28 germ pores near the septum.

FIGS. 31, 32. Two-celled teleutospores of *G. biseptatum*.

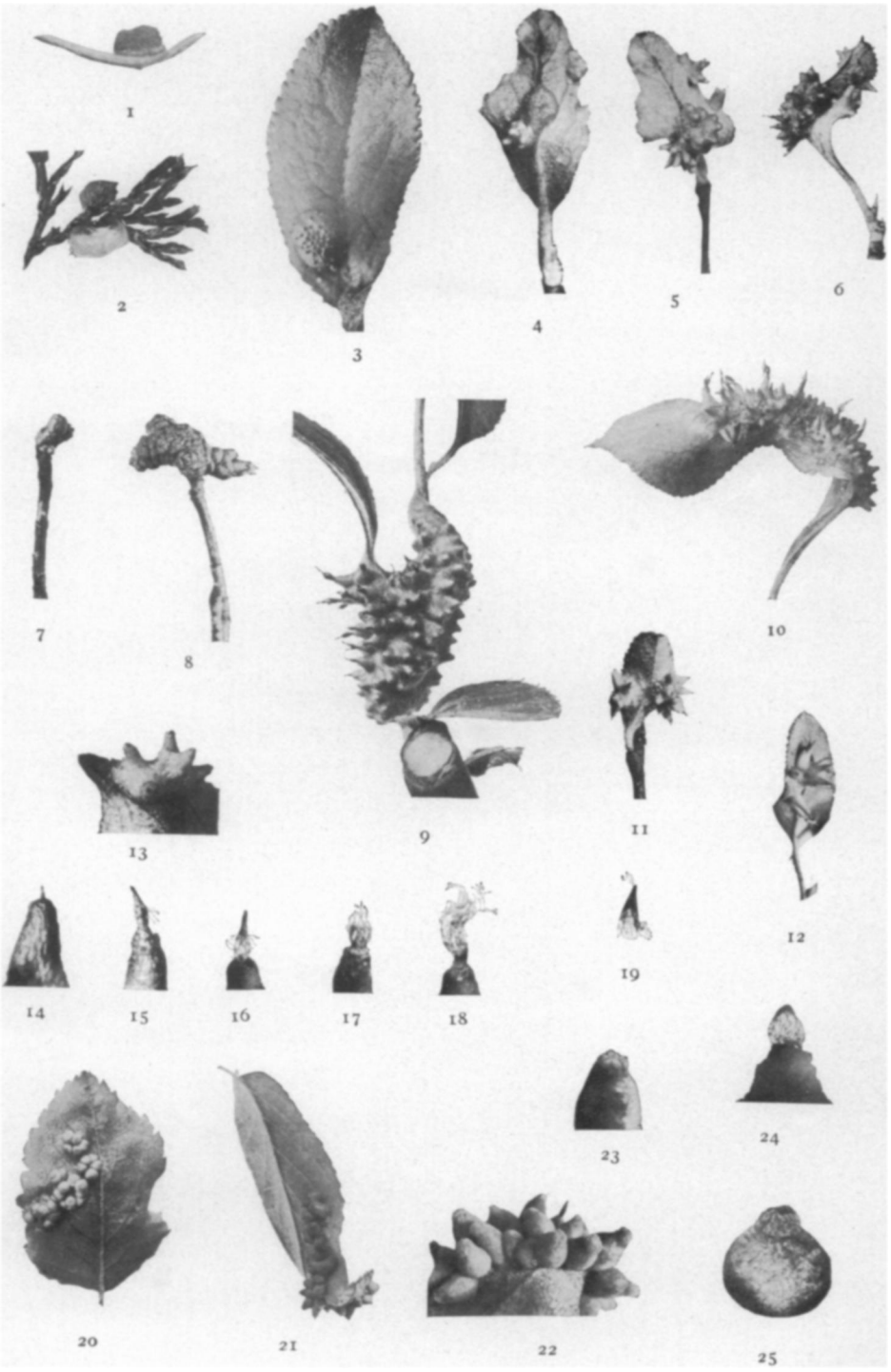
FIGS. 33–38. Various stages in the germination of spores and formation of promycelium and sporidia of *G. fraternum*.

FIGS. 39, 40. Germination of sporidia and formation of secondary spores.

FIG. 41. A peridial cell from *G. fraternum* (*Roestelia transformans*) on *Aronia*.

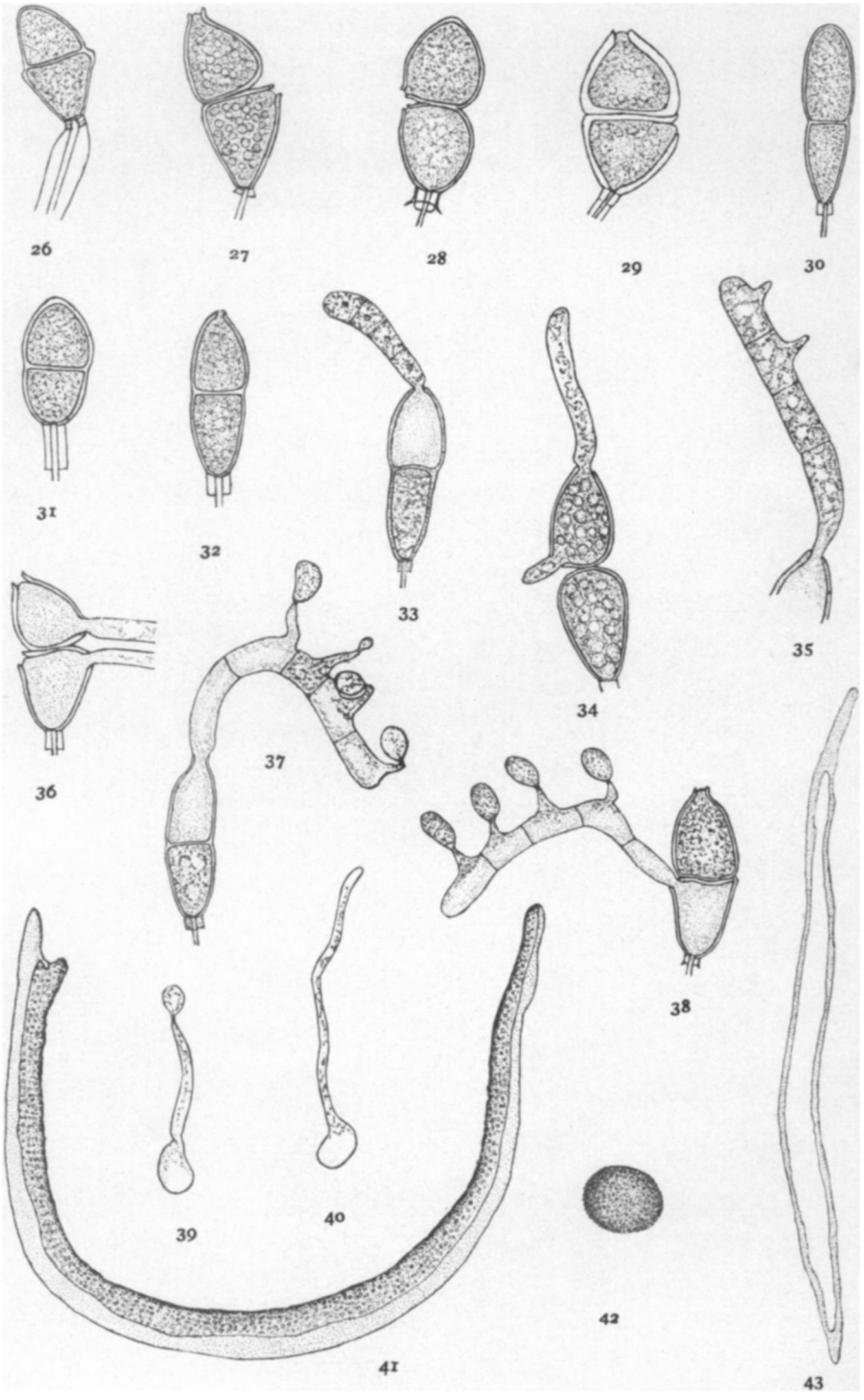
FIG. 42. Spore from the same aecidium.

FIG. 43. A peridial cell from *G. fraternum* on *Amelanchier*.



DODGE

GYMNOSPORANGIUM



DODGE

GYMNOSPORANGIUM